SMALL *NAIADITES OBESUS* FROM THE CALCIFEROUS SANDSTONE SERIES (LOWER CARBONIFEROUS) OF FIFE

by G. M. BENNISON

ABSTRACT. Small specimens of *Naiadites* occur at two horizons in the Calciferous Sandstone Series of Eastern Fife. At one horizon the small shells constitute an indigenous 'life-assemblage' (now a fossil community), and are described as dwarfed, whereas at the other the shells are exotic, comprising a fossil assemblage that should be termed a 'pebble necrocoenosis'. Variation is illustrated, and the affinities of these small *Naiadites* are re-examined. All are referred to the species *N. obesus s.l.*

LEITCH (1942, p. 219) makes reference to collections of 'dwarfed' *Naiadites* from a shaly mudstone above the No. 9 Limestone, Randerstone (Kirkby 1901), and from the shore near the Rock and Spindle, St. Andrews. The latter collection was made by Mr. W. Manson of the Geological Survey.

Although Kirkby (1901) measured the entire shore section at Randerstone, and Kirk (1925) mapped the Rock and Spindle shore in very great detail, the relative positions of these two *Naiadites*-bearing beds cannot be determined, and the faunal relationships examined by the writer suggest that their tentative correlation by Leitch cannot be sustained.

1. *Fauna above the No. 9 Limestone, Randerstone.* In a shell bed above the No. 9 Limestone, Randerstone, the disposition of the small *Naiadites*, mean L = 12·6 mm. (figured by Leitch 1942, pl. iii and fig. 9) relative to a large *Naiadites obesus* fauna is remarkable (text-fig. 1). The small *Naiadites* make their appearance 3 feet higher than the large forms which are immediately above the limestone. There is no abrupt replacement of one by the other: from 3 feet to 3 feet 6 inches above the limestone the two occur in close proximity. In the highest 6 inches of the shell bed only the small form is found.

Histograms showing the distribution of length of shell from three samples and from the samples combined (text-fig. 2) clearly confirm the presence of two forms, the latter being bimodal. The small shells, sample 3, have a very small range of length (an indication of sorting by waves or currents), and therefore do not comprise a 'life assemblage' or fossil community. Shells of *N. obesus* from the lowest 3 feet of the bed (sample 1) have, on the other hand, a wide range of length, both juvenile and gerontic specimens being present, and represent a fossil community (see Craig 1953, p. 547).

The large and small forms differ in the nature of their preservation. The 'dwarfed' form usually comprising both valves, which are tumid and little affected by crushing ('solids'). The 'normal' *Naiadites obesus*, on the contrary, is flattened, often comprising single valves only (as far as one can tell), in a beautiful state of preservation despite the delicate and fragile postero-dorsal area. The 'dwarfed' form, however, is frequently incomplete; in no case could the postero-dorsal region be found adhering to the adjacent shale. The normal *N. obesus* cannot have been far removed from its ecological station and the shells appear to constitute a life assemblage; but the associated 'dwarfed'

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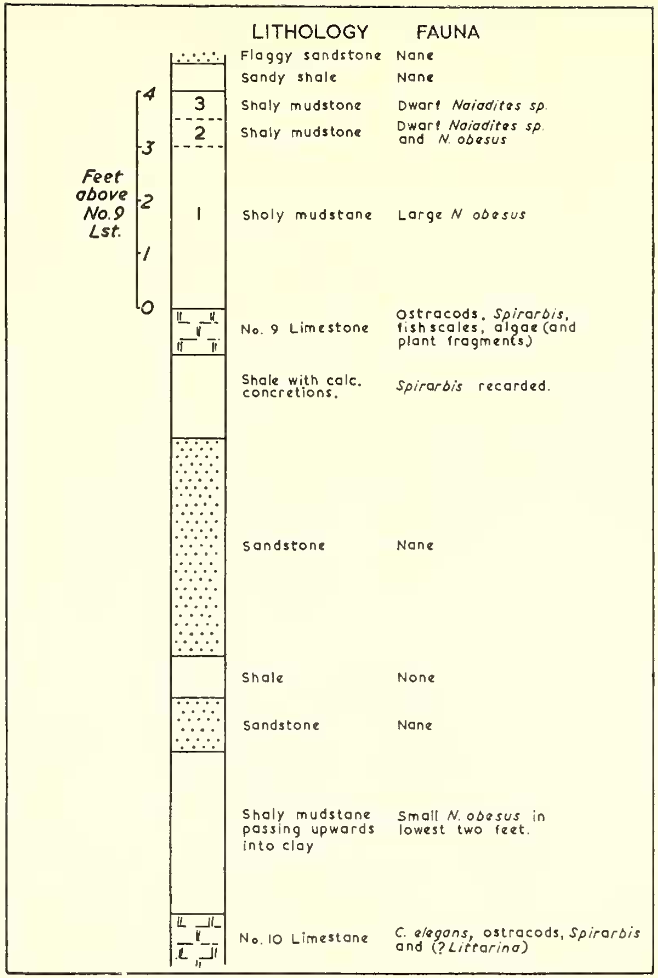
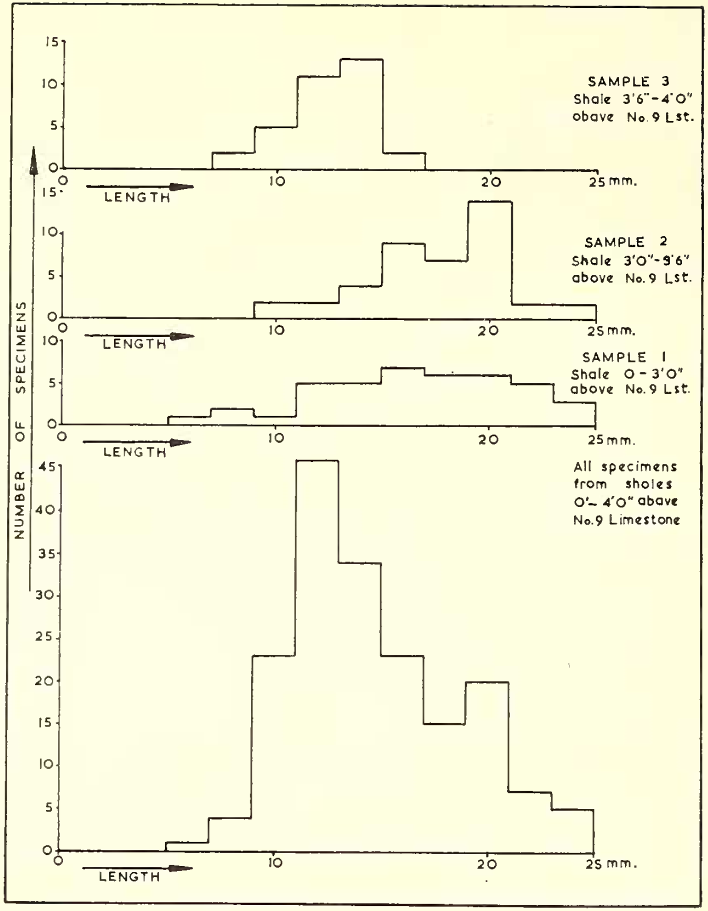
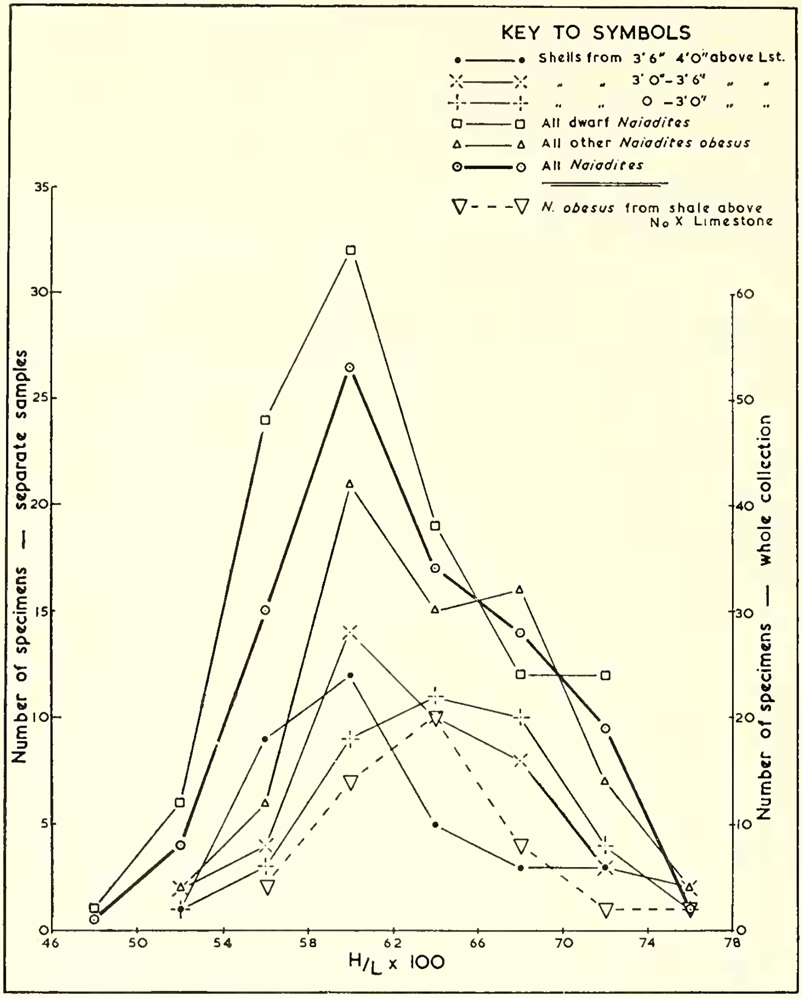


TEXT-FIG. 1. Detailed succession above Nos. 9 and 10 Limestones, Randerstone.



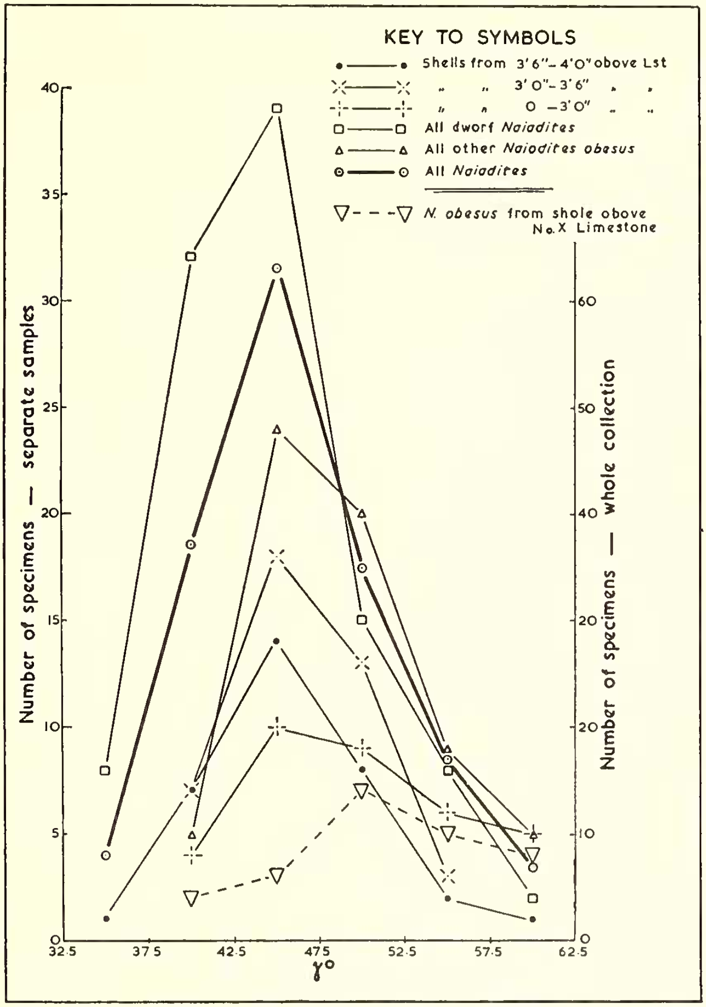
TEXT-FIG. 2. Histograms showing distribution of the length of shells from three collections of *N. obesus s.l.*

form may have drifted into the bed. These ecologically foreign shells, which may be termed exotic, present a problem, for they have remained articulated. The infilling of ironstone protected the shells from the effects of compaction of the sediment. Some specimens retained their shape despite the removal by erosion of the shell material. The continuance of *N. obesus* through a further 6 inches of strata after the appearance of the 'dwarfed' form suggests that the incoming of the latter is not indicative of a change in the biotype.



TEXT-FIG. 3. Graphs to show the ratio of length (L) to height (H) in collections of *Naiadites* from a bed above the No. 9 Limestone, Randerstone.

Since the distinction between 'dwarfed' or small *Naiadites* and normal *N. obesus*, as used above, is largely dependent on visual recognition of the two forms, and hence is subjective, frequency polygons have been drawn on the basis of stratigraphical samples (text-figs. 3 and 4). Only those for H/L and γ (see Trueman and Weir 1955, p. 212) are here reproduced. The difficulties of making comparison between crushed and uncrushed *Naiadites* have been explored (Bennison 1959, pp. 48–59), and crushing shown to result in a generally lower value for H/L and γ (the coefficient of correlation between them is high, *c.* 0·5). The observed differences, both of mode and range of variation of H/L,



TEXT-FIG. 4. Graphs to show the variation in the value of the angle γ in collections of *Naiadites* from a bed above the No. 9 Limestone, Randerstone.

cannot therefore be ascribed to the effects of crushing of the normal *N. obesus*, for this would tend to produce a difference contrary to that observed. The difference of values of H/L might be a function of growth, since the direction of maximum marginal increment changes during ontogeny, as shown by the tilted growth lines. That this may reflect a change in the attitude of the shell to the byssus is discussed in a later section: the immediate consideration is whether the difference in values of H/L in the two forms indicates a diagnostic criterion of specific or varietal stature; but the observed differences in H/L cannot reliably be attributed to either growth changes or crushing, since the reductions in H/L tend to 'cancel out'.

2. *Dwarfed* Naiadites *from a bed near the Rock and Spindle*. Small shells (mean L = *c.* 13 mm.), referable to *Naiadites*, are common in a bed of hard grey shaly mudstone exposed in a low cliff, 35 yards to the south of the Rock and Spindle vent. The bed is at least 3 feet thick; its stratigraphical position is uncertain, although this shore section is assigned by Kirk (1925) to a high position in the Calciferous Sandstone Series, by virtue of the correlation of his 'Marine Fossil Bed III' with the 'Encrinite Bed' of Kirkby's main Pittenweem-Anstruther section (Kirkby, in Geikie, 1902, p. 87). The bed now in question outcrops between Kirk's Marine Fossil Beds III and IV and, unless the faults bounding it are of very considerable magnitude, it must be much higher in the succession than the bed above the No. 9 Limestone, Randerstone. With Kirk (op cit., p. 369), the writer rejects Kirkby's suggestion (1880, p. 136) that Kirk's Marine Fossil Bed III (the *Myalina* Limestone of the Geological Survey) is equivalent to Kirkby's No. 3 Limestone of the Randerstone shore section.

The mode of occurrence of the shells in this bed near the Rock and Spindle is distinctive, in that a large number comprise both valves, agape but not disarticulated. Detailed work has shown that there is a reduction in size of shell (mean length) at the top of the shell bed before the final disappearance of *Naiadites*.

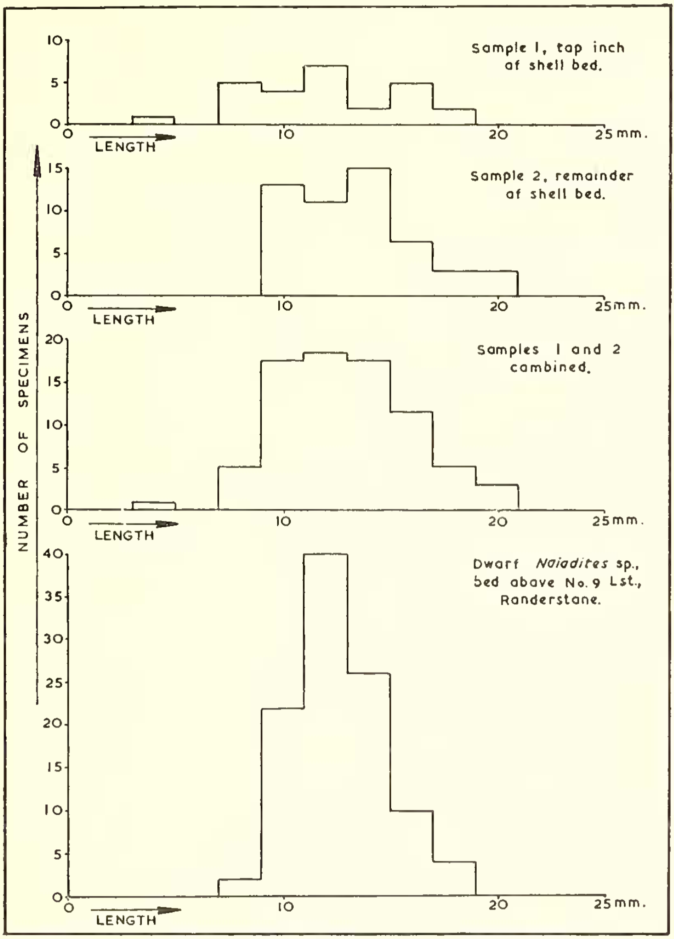
Frequency polygons for H/L, DM/L, A/L, the angle γ and the angle β show modal values closely comparable with those of collections of *N. obesus*. The modal value of H/L is low (*c.* 60 per cent.), and the anterior end is relatively long, as would be expected in a collection of small shells. Further, regression of the angle γ on H/L, as well as the regression of the angle β on DM/L, show no appreciable difference from the corresponding regression in collections of *N. obesus* of normal size. It is concluded that this is an assemblage of *N. obesus s.l.* which is exceptional only in size; in the high percentage of articulated shells; and in the wide range of variation in shape of shell. Broadhurst (1959, p. 532) considers that in any assemblage the presence of a high percentage of shells which have not become disarticulated may be taken as evidence of freedom from turbulence and sorting, unless the ratio of articulated/disarticulated shells is due to a variation in the resistance of the hinge mechanism. Boucot (1953, p. 32) suggests that a single assemblage with a large percentage of articulated specimens, of a species with easily disarticulated shells, may represent a 'life assemblage'.

Histograms showing the distribution of length of shell in samples from the main part of the shell bed and the top inch, and their summation (text-fig. 5) provide evidence of the probability of a life assemblage. The histogram for the main sample has the characteristic right skew, indicative of a life assemblage, but the sample from the top inch of the bed shows an irregular distribution of length of shell. Summing the two samples gives the typical 'bell-shaped' distribution curve, which is found in so many samples of fossil 'populations', which are aggregations or assemblages (*see* Craig loc. cit.).

3. *A small form of* N. obesus *from a bed above the No. 10 Limestone, Randerstone*. Small *N. obesus* (mean L = 15 mm.) occurs in a 2-foot bed of dark shaly mudstone immediately above the No. 10 Limestone, Randerstone (text-fig. 1). *N. obesus* here chiefly comprises disarticulated flattened valves, intermediate in size between the smaller shells, discussed

above, and the larger *N. obesus*, which commonly occurs in the Calciferous Sandstone Series of this area. In this bed, a decrease in size of the shells found near the top is associated with a decrease in numbers accompanied by a lithological change.

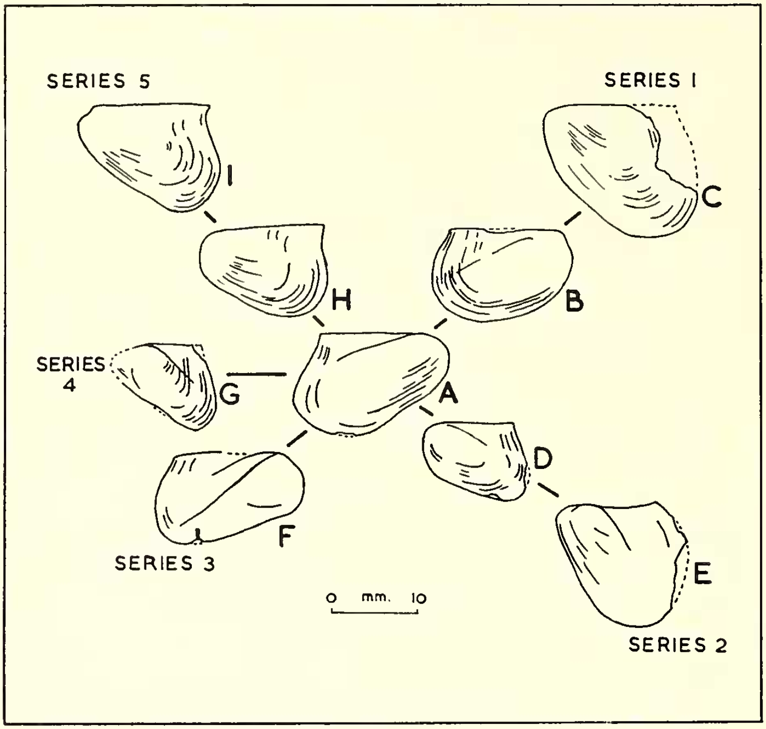
Maximum observed size is, by itself, no criterion of dwarfing, and in a bed of shale succeeding the No. 3 Limestone, Randerstone *N. obesus* attains its greatest size—the shells are somewhat larger than the topotype material from the Water of Leith (Trueman and Weir 1956, p. 262); in other occurrences it shows some reduction in size. The term dwarfing, used conservatively—following Tasch (1953), who restricts it to forms in which there is evidence of failure to attain the normal size of adult shells, as a result of stunting due to adverse ecological conditions—can seldom be applied. Certainly, in the case of the small shells described in section 1, there is no evidence of such stunting.



TEXT-FIG. 5. Histograms showing distribution of the length of shells in two samples of *N. obesus* from a bed near the Rock and Spindle, Kinkell shore, St. Andrews, compared with a sample from a bed above the No. 9 Limestone, Randerstone.

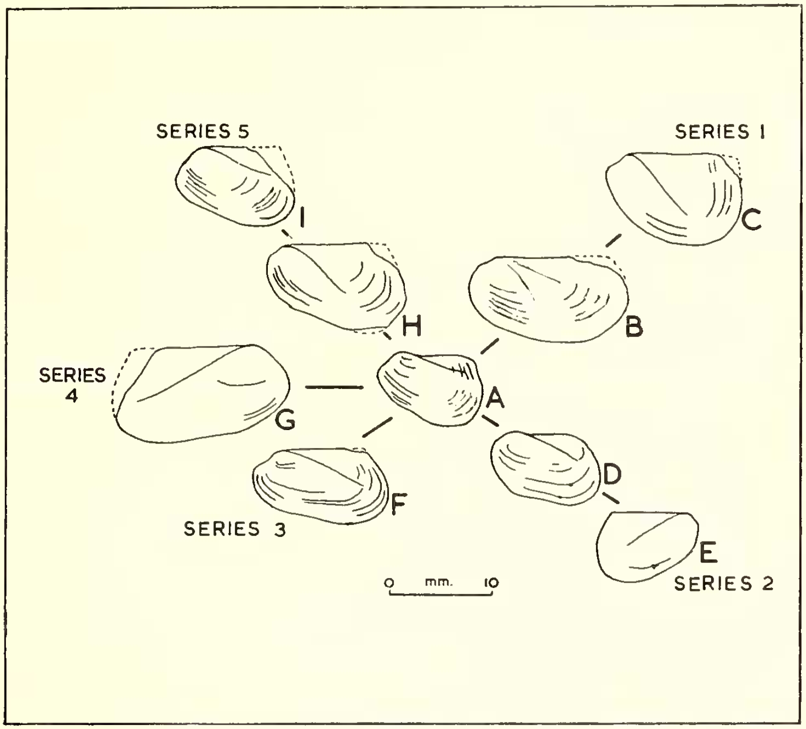
The other instances of small *Naiadites*, described in sections 2 and 3, are examples of either the failure of individuals to attain full size, although adult, or failure to reach the adult stage. If the former, we have true examples of dwarfing. The rather low values for H/L are inconclusive, but the distribution of length of shell points to an example of dwarfing in the bed near the Rock and Spindle.

4. *The specific identity of the small* Naiadites. Many of the small shells are similar to typical *Naiadites obesus*, although smaller, but Leitch (1942, p. 219) has raised the problem of their generic identity—as well as their specific identity—because of the presence of *Anthraconaia*-like variants. Leitch, for purposes of description, divides the dwarfed shells into two groups, while agreeing that simulants of *Anthraconaia* '. . . can be intergraded to other members of the community which are more naiaditiform and can in turn be intergraded with *Naiadites obesus*'. Frequency polygons drawn for the ratios H/L, DM/L, and A/L, as well as for the angles γ and β, are all unimodal, establishing that variation is continuous from one extreme to the other.



TEXT-FIG. 6. Pictograph showing variation in the shape of shells of *N. obesus s.l.* from shaly mudstone above the No. 9 Limestone, Randerstone. (i) Excluding 'dwarfed' shells.

Having shown that separation of the small and the normal *Naiadites* is not arbitrary, it is now necessary to show that both are referable to the species *N. obesus s.l.* The regression of γ on H/L, as well as the correlation between γ and H/L, is similar in both cases, also pictographs (text-figs. 6 and 7) supplement the evidence of the graphs. In both cases, the figured intergrades are arranged into the series used by Leitch (op. cit., p. 212) so that close comparison can be made between the two collections, and the conclusion drawn that the small shells may also be referred to *N. obesus s.l.* Variation in *N. obesus* from the bed above the No. 9 Limestone is illustrated by means of figured intergrades (text-fig. 6) and comparison with Leitch's fig. 5 shows that variants representing most of his series of intergrades can be found. Similarly, variation in the small *Naiadites* from the same bed is illustrated by selected intergrades (text-fig. 7) arranged into identically defined series. The figured intergrades of text-figs. 6 and 7 are not identical, but are closely similar: the purpose of the pictographs is not to show that the collections of shells are indistinguishable, but to establish that the range of variation in shape of shell is closely comparable.



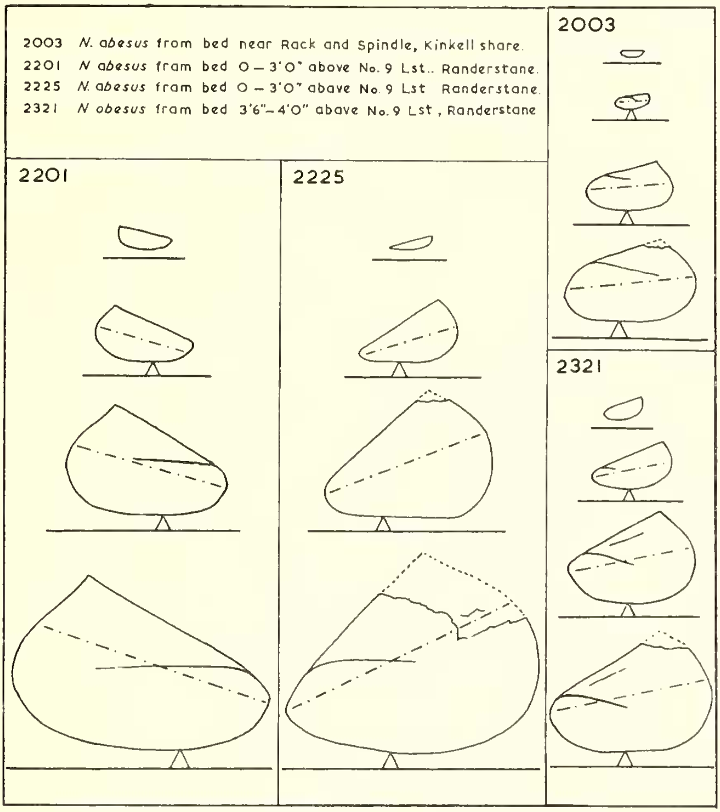
TEXT-FIG. 7. Pictograph showing variation in the shape of shells of *N. obesus s.l.* from shaly mudstone above the No. 9 Limestone, Randerstone. (ii) 'Dwarfed' shells only.

Newell (1940, pp. 291, 294) has shown anterior musculature to be of some importance in the identification of genera of the Mytilacea. The writer has seen little evidence of the musculature of the small *Naiadites*, but Weir (1945, p. 319) describes the relatively large anterior adductor muscle observed in one specimen. Moulds do not commonly show muscle scars and it is probable that the muscles may not have been deeply inserted. The large size of the anterior adductor described by Weir, and the absence of a deep anterior muscle pit, are not typical of *Naiadites*, but do not preclude these shells from reference to that genus. The position of the umbo is the most important single factor in the determination of genera of Myalinidae. In *Naiadites* the sinuous carina (or umbonal ridge) has a forward twist carrying the umbones towards the anterior end (thus distinguishing these shells from the small *Curvirimula* [*Anthracouauta*] which are known from the Calciferous Sandstone Series (see Weir 1945, p. 318; 1960, pp. 301, 314–20)) but the umbones are never terminal, except in a few shells which show clear signs of distortion due to crushing; on the contrary, the small *Naiadites* possesses an unusually long anterior end (the modal value is *c*. 16 per cent). In general, the anterior end of *Naiadites* is short—Trueman and Weir give a figure of 10–12 per cent. of the length; A/L commonly exceeds this figure in the case of *N. obesus*, as well as in these small specimens, and it seems probable that this early *Naiadites* may not have been derived from an ancestral form with an amphidetic ligament since, even at this early date (Visean, Stage B, Currie 1954), *Myaliua* and *Naiadites* were clearly differentiated. Although *N. obesus* is referable to *Naiadites* as interpreted by Trueman and Weir, its relationship to later forms is not satisfactorily established. A long period elapsed between the demise of *N. obesus* and the appearance of Westphalian species, with only *N. tumidus*, the Namurian form, providing a link in time. It is not suggested that *N. obesus* provides evidence of the origin of the genus as a whole, and Newell (1942, p. 72) suggests that Westphalian *Naiadites* may have been derived from a more distinctly amphidetic Devonian form.

Weir (1945, pp. 321 and 323) suggests that *Naiadites* of the *obesus-tumidus* group is probably not derived from *Myaliua*, and the relatively long anterior end of *N. obesus* appears to preclude its secondarily redeveloped origin. *N. obesus*, in the early growth stages, is less asymmetrical than in the adult form: in spat of *Naiadites* generally, the umbones are almost central. During ontogeny there is a gradual change is the direction of maximum marginal increment, as shown by the tilted growth-lines, and this may reflect a change in the attitude of the shell to the byssus. The angular relationship between the shell axis (Jackson 1890, p. 509, footnote 3) and the presumed byssal axis has been studied in numbers of adult shells from assemblages of small *N. obesus* and normal *N. obesus*. An attempt to deduce from growth-lines the change in angular relationship during ontogeny has also been made (text-fig. 8). In assemblages of small *N. obesus*, where the modal value of H/L is rather low, the angle between the shell axis and the byssal axis ranges from 90° to 110°; Weir (1945, p. 319) deduces the range of variation from a re-examination of Leitch's material. The study of additional material has not extended the known range of variation, but has confirmed Weir's figures. In larger *N. obesus* the angle varies from something less than 100° to 120°, thus certainly overlapping the lower figure for *N. tumidus* given by Weir (loc. cit.). In young individuals the angle between the shell axis and the byssal axis is a right angle, and the ventral margin is parallel, or very nearly so, to the hinge-line. As growth proceeds, the angle gradually increases, but in 'dwarfed' shells the process is not continued as far as in large *N. obesus*. Also, the angle of obliquity in 'dwarfed' shells is less than in large *N. obesus*. The implication of these observations is that 'dwarfed' individuals are *N. obesus* in which development has been terminated prematurely—and so they are not truly dwarfed.

The small *Naiadites* from the bed above the No. 9 Limestone, Randerstone, described in section 1, is referable to the species *N. obesus s.l. Authraconaia*-like variants are present though not numerous; this is true of all assemblages of *N. obesus* examined by the writer. The presence of *Curvirimula* [*Anthraconauta* pars.] cannot be confirmed. Only in distorted shells have terminal umbones been found. Evidence that the shells have been sorted and washed into the bed implies that they are not dwarfed, but comprise what Tasch (1953, p. 403) describes as a 'pebble necrocoenosis'.

The small shells, described in section 2 from the bed near the Rock and Spindle, comprise *N. obesus s.l.* Here, it is exceptional only in the small size and high percentage of articulated shells. A large number of shells (over ninety) were obtained; the range of variation in shape appears to be unusually great, a circumstance which may be in part attributable to the size of the sample. Variation is illustrated by pictograph (text-fig. 9), but since one of the shortcomings of Leitch's figure (1942, p. 213, fig. 5) is that it includes completely flattened as well as uncrushed tumid specimens, the series of figured intergrades are here redefined as follows:



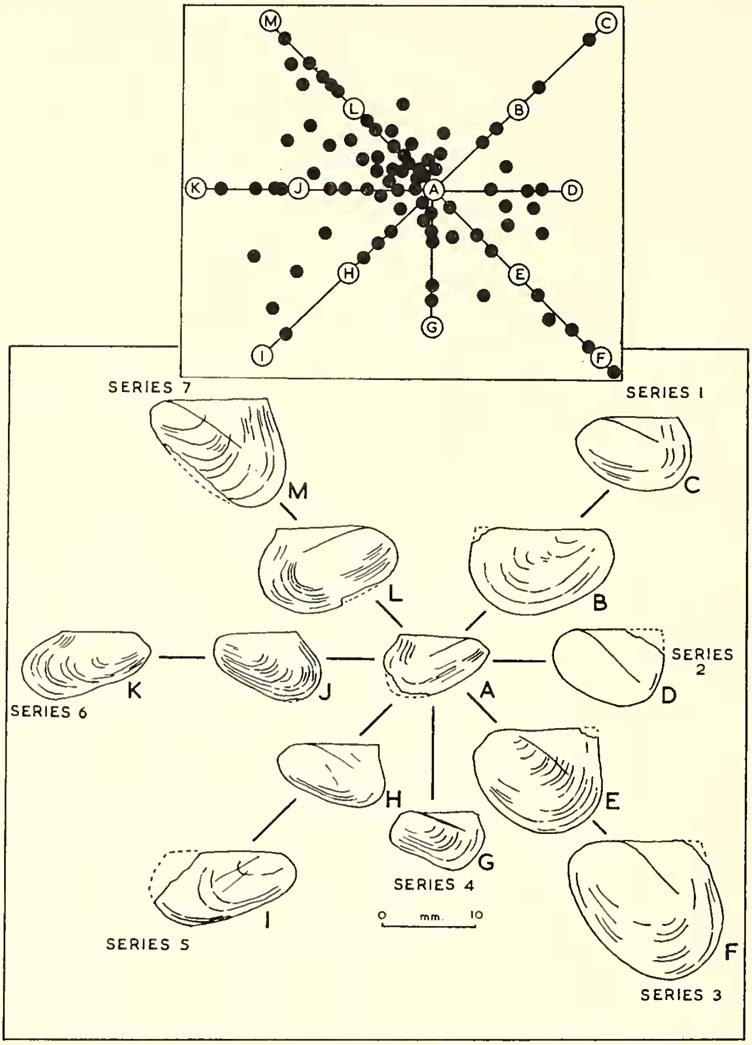
TEXT-FIG. 8. The relationship of byssal axis to shell axis in some specimens of *Naiadites obesus s.l.*

> *Series 1* (9 A, B, C) is characterized by shells with a high value for H/L, a low value for β and a rounded ventral margin.
>
> *Series 2* (9 A, D) includes shells with a rather low value for H/L and with β a little over 90°.

Series 3 (9 A, E, F) includes shells with a high value for H/L, in which the anterior-ventral slope becomes nearly parallel to the posterior end.

Series 4 (9 A, G) includes forms resembling *Anthraconaia.*

Series 5 (9 A, H, I) includes sub-triangular shells with a low value for H/L.



TEXT-FIG. 9. Pictograph showing variation in the shape of shells of *N. obesus s.l.* from a bed near the Rock and Spindle, Kinkell shore, St. Andrews.

Series 6 (9 A, J, K) includes shells with a high value for the angle β.

Series 7 (9 A, L, M) comprises highly carinate forms showing a tendency for the anterior-ventral slope to become nearly straight.

The distribution of the assemblage relative to the figured intergrades is shown in the inset of text-fig. 9. The latter provides the best illustration of shape variation, excluding the grosser effects due to flattening, not merely in this particular assemblage, but in *N. obesus s.l.*

5. *Lithological observations.* A modification of a technique using bakelite cement, described by Legette (1928, pp. 551–7), was employed in making thin sections. The matrices of the shell beds which include *N. obesus* appear to contain little quartz, although high magnification reveals many virtually ultramicroscopic grains (less than 10 μ), and its presence in the fine fraction was confirmed by X-ray analysis. The sample from the top inch of the shell bed near the Rock and Spindle proved exceptional, revealing an increase in the coarseness of the silt to 25 μ. It appears that, in this case, the decrease in size of shell can be related to a change in conditions of sedimentation, that stunting occurred as a result of adverse conditions—since there is no evidence of sorting—and that it is an example of a dwarfed fauna.

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G. M. BENNISON
Department of Geology,
The University,
Birmingham, 15.

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